

A worldwide list of hermit crabs and their relatives (Anomura: Paguroidea) reported as hosts of Isopoda Bopyridae

JOHN C. MARKHAM

Arch Cape Marine Laboratory, 108 W. Markham Avenue, Arch Cape, OR 97102-0105, USA (jmarkham@seasurf.com)

Abstract

Markham, J.C., 2003. A worldwide list of hermit crabs and their relatives (Anomura: Paguroidea) reported as hosts of Isopoda Bopyridae. In: Lemaitre, R., and Tudge, C.C. (eds), Biology of the Anomura. Proceedings of a symposium at the Fifth International Crustacean Congress, Melbourne, Australia, 9–13 July 2001. *Memoirs of Museum Victoria* 60(1): 71–77.

Hermit crabs and their relatives in the anomuran superfamily Paguroidea are among the most frequently reported hosts of bopyrid isopods, all species of which are parasites of decapod crustaceans in general. This report serves, for the first time, to collect the widely scattered records of paguroid infestation into a single list with both host and parasite names updated to conform with the currently accepted nomenclature; each entry includes the geographical locality for the occurrence of each species of parasite on each species of host and the citation of the publication in which it was reported. The known host paguroids are in the Diogenidae (48 species plus 3 others not identified to species), Lithodidae (6), Paguridae (52 + 7), and Parapaguridae (3 + 1). Their parasites belong to three bopyrid subfamilies, the Pseudioninae (32 species occurring in the branchial chambers of hosts), the Athelginae (41 species clinging to the abdomens of their hosts), and the Bopyrophryxinae (one species attached simultaneously to branchiae and abdomen of their hosts).

Keywords

Crustacea, Anomura, Paguroidea, Isopoda, Bopyridae, species list

Introduction

The epicaridean isopod family Bopyridae contains just over 500 described species worldwide in ten subfamilies, all of which parasitise decapod crustaceans as adults. With one exception, all known species are external parasites. Seventy-four are known to infest hosts in the anomuran superfamily Paguroidea.

So far, there are reports of 48 species of Diogenidae plus three others identified only to genus serving as bopyrid hosts, six species of Lithodidae, 52 species of Paguridae plus seven identified only to genus or family, and three species of Parapaguridae plus one identified only to genus. Their parasites belong to three bopyrid subfamilies: Pseudioninae, the largest and probably most primitive subfamily, whose species are branchial parasites mainly of Anomura in general; the rather small and evidently fairly advanced subfamily Athelginae, all of whose species are dorsoabdominal parasites of paguroids alone; and the monotypic subfamily Bopyrophryxinae, whose single species is simultaneously a branchial and abdominal parasite of a parapagurid. Published records of the occurrences of paguroid-infesting bopyrid isopods have been very widely scattered; it is hoped that this compilation, by bringing them all together for the first time, will be useful to readers seeking information about both the hosts and their parasites.

The following is a list of all known Paguroidea hosts, their

recorded Bopyridae parasites, their known localities and references reporting them. The families of the superfamily Paguroidea are in accordance with the most recently published classification of Martin and Davis (2001). The names of the hosts and parasites have been corrected, as needed, to conform with the most current taxonomic opinion, so they are not necessarily those previously used in the original publications.

Superfamily Paguroidea

Coenobitidae

No records known.

Diogenidae

Allodardanus bredinii Haig and Provenzano, 1965: *Parathelges tumidipes* Markham, 1972, Athelginae; Bermuda (Markham, 1978).

Calcinus elegans (H. Milne Edwards, 1848): *Parapagurion calcinicola* Shiino, 1933, Pseudioninae; Seto, Japan (Shiino, 1933).

C. morgani Rahayu and Forest, 1998: *Propseudione rhombosoma* Shiino, 1933, Pseudioninae; Irian Jaya, Indonesia (Haig and Ball, 1988). *Pseudostegias macdermotti* Williams and Boyko, 1999, Athelginae; Bali, Indonesia (Williams and Boyko, 1999).

C. laevimanus (Randall, 1839): *Propseudione rhombicosoma* Shiino, 1933, Pseudioninae; Seto, Japan (Shiino, 1933). *Parathelges weberi* Nierstrasz and Brender à Brandis, 1923, Athelginae; Maiwara, Papua New Guinea (Danforth, 1971), Irian Jaya, Indonesia (Haig and Ball, 1988).

C. latens (Randall, 1839): *Pseudione calcinii* (Shiino, 1958), Pseudioninae; Japan (Shiino, 1958).

C. lineapropodus Morgan and Forest, 1991: *Parapagurion calcincola* Shiino, 1933, Pseudioninae; Irian Jaya, Indonesia (Haig and Ball, 1988). *Anathelges muelleri* Nierstrasz and Brender à Brandis, 1931, Athelginae; Irian Jaya, Indonesia (Haig and Ball, 1988). *Athelges* sp., Athelginae; Irian Jaya, Indonesia (Haig and Ball, 1988).

Ciliopagurus strigatus (Herbst, 1804): *Athelges* sp., Athelginae; Irian Jaya, Indonesia (Haig and Ball, 1988).

Clibanarius albidigitus Nobili, 1901: *Bopyrissa magellanica* Nierstrasz and Brender à Brandis, 1931, Pseudioninae; Pacific coast, Costa Rica (Nierstrasz and Brender à Brandis, 1931).

C. antillensis Stimpson, 1862: *Asymmetrione clibanarii* Markham, 1975, Pseudioninae; Caribbean coast, Colombia (Markham, 1988).

C. bimaculatus (De Haan, 1849): *Asymmetrione asymmetrica* (Shiino, 1933), Pseudioninae; Tanabe Bay, Japan (Shiino, 1933). *Bopyrissa pyriforma* (Shiino, 1958), Pseudioninae; Hong Kong (Markham, 1982). *Pseudione clibanaricola* Shiino, 1933, Pseudioninae; Tanabe Bay, Japan (Shiino, 1933). *Pseudostegias setoensis* Shiino, 1933, Athelginae; Seto, Japan (Shiino, 1933); Hong Kong (Markham, 1982).

C. digueti Bouvier, 1898: *Pseudione* sp., Pseudioninae; Gulf of California, Mexico (Brusca, 1980).

C. englaucus Ball and Haig, 1972: *Asymmetrione asymmetrica* (Shiino, 1933), Pseudioninae; Irian Jaya, Indonesia (Haig and Ball, 1988).

C. erythropus (Latreille, 1818): *Bopyrissa fraiseii* (Carayon, 1943), Pseudioninae; Arcachon, France (Bourdon, 1968). *Parathelges cardonae* R. and M. Codreanu, 1968, Athelginae; Corsica (Codreanu, 1968); Balears Islands (Bonnier, 1900); Mediterranean coast of Africa (Codreanu, 1961). *Parathelges racovitzae* Codreanu, 1940, Athelginae; Corsica (Altès, 1962).

C. merguiensis de Man, 1888: *Bopyrissa liberorum* Markham, 1985, Pseudioninae; Phuket, Thailand (Markham, 1985b). *Pseudostegias dulcilacuum* Markham, 1982, Athelginae; Phuket, Thailand (Markham, 1985b).

C. padaverensis de Man, 1888: *Pseudostegias setoensis* Shiino, 1933, Athelginae; Phuket, Thailand (Markham, 1985b).

C. signatus Heller, 1861: *Asymmetrione shiinoi* Codreanu et al., 1965, Pseudioninae; Red Sea (Codreanu et al., 1965).

C. striolatus Dana, 1852: *Pseudostegias setoensis* Shiino, 1933, Athelginae; Taiwan (Shiino, 1958).

C. taeniatius (H. Milne Edwards, 1848): *Pseudostegias setoensis* Shiino, 1933, Athelginae; Queensland, Australia (Dunbar and Coates, 2000).

C. tricolor (Gibbes, 1840): *Asymmetrione clibanarii* Markham, 1975, Pseudioninae; Florida, USA; Bahamas; Caribbean coast, Colombia (Markham, 1988). *Bopyrissa wolffi* Markham, 1978, Pseudioninae; Bermuda; Florida, USA; Bahamas; Quintana Roo, Mexico; Puerto Rico (Markham,

1978; Markham et al., 1990). *Parathelges occidentalis* Markham, 1972, Athelginae; Florida, USA; Bahamas; Quintana Roo, Mexico (Markham, 1972). *Stegias clibanarii* Richardson, 1904, Athelginae; Bermuda; Caribbean (Markham, 1979).

C. virescens (Krauss, 1843): *Pseudostegias setoensis* Shiino, 1933, Athelginae; Queensland, Australia (Dunbar and Coates, 2000). Unidentified, Indian Ocean coast, South Africa (Barnard, 1950).

C. vittatus (Bosc, 1802): *Bopyrissa wolffi* Markham, 1978, Pseudioninae; North Carolina and Texas, USA (Markham, 1978).

Clibanarius sp. aff. *longitarsus* (De Haan, 1849): *Pseudione novaeguineensis* Danforth, 1971, Pseudioninae; Maiwara, Papua New Guinea (Danforth, 1971).

Clibanarius sp. aff. *tricolor* (Gibbes, 1840): *Asymmetrione clibanarii* Markham, 1975, Pseudioninae; Ascension Island (Markham, 1978).

Clibanarius sp.: *Asymmetrione* sp., Pseudioninae; Puntarenas, Costa Rica (Markham, 1975). *Bopyrella magellanica* Nierstrasz and Brender à Brandis, 1931, Pseudioninae; Puntarenas, Costa Rica (Nierstrasz and Brender à Brandis, 1931).

Clibanarius sp.: *Pseudione brandaoi* Brian and Darteville, 1941, Pseudioninae; Congo (Brian and Darteville, 1941).

Clibanarius sp.: *Pseudostegias atlantica* Lemos de Castro, 1965, Athelginae; Ceará and Alagoas, Brazil (Lemos de Castro, 1965).

Dardanus arrosor (Herbst, 1796): *Asymmetrione dardani* Bourdon, 1968, Pseudioninae; Atlantic coast, Morocco (Bourdon, 1968). *Parathelges carolii* Codreanu, 1968, Athelginae; Naples, Italy (Codreanu, 1968).

D. fucosus Biffar and Provenzano, 1972: *Parathelges tumidipes* Markham, 1972, Athelginae; Jamaica (Markham, 1972).

D. gardineri Alcock, 1905: *Athelges aegyptius* Codreanu et al., 1965, Athelginae; Red Sea (Codreanu et al., 1965). *Athelges caudalis* Barnard, Athelginae; Inhambane, Mozambique (Barnard, 1955).

D. megistos (Herbst, 1804): Athelginae, unidentified; unspecified locality, Australia (Jones and Morgan, 1994).

Dardanus sp.: *Pagurion tuberculata* Shiino, 1933, Pseudioninae; Tanabe Bay, Japan (Shiino, 1933).

Diogenes edwardsii (De Haan, 1849): *Bopyrissa pyriforma* (Shiino, 1958), Pseudioninae; Mie Prefecture, Japan (Shiino, 1958); Hong Kong (Markham, 1982); southwest Korea (Kim and Kwon, 1988). *Athelges takanoshimensis* Ishii, 1914, Athelginae; Hong Kong (Markham, 1982). *Pseudostegias dulcilacuum* Markham, 1982, Athelginae; Hong Kong (Markham, 1982).

D. merguiensis de Man, 1888: *Bopyrissa dawydoffi* (Codreanu and Codreanu, 1963), Pseudioninae; Thanh Hoa, Vietnam (Codreanu and Codreanu, 1963).

D. pugilator (Roux, 1829): *Bopyrissa diogeni* (Popov, 1927), Pseudioninae; Black Sea; Channel Islands (Bourdon, 1968). *Athelges paguri* (Rathke, 1843), Athelginae; Roscoff, France (Bourdon, 1967). *Parathelges racovitzae* Codreanu, 1940, Athelginae; Black Sea, Romania (Codreanu, 1940).

Isocheles pilosus (Holmes, 1900): *Asymmetrione ambodis-torta* Markham, 1985, Pseudioninae; California, USA (Markham, 1985a).

Paguristes anahuachis Glassell, 1938: *Pseudione* sp., Pseudioninae; Gulf of California, Mexico (Brusca, 1980).

P. emerita (Linnaeus, 1767): *Athelges pelagosae* Babić, 1912, Athelginae; Adriatic Sea (Babić, 1912).

P. hummi Wass, 1955: unidentified. Florida, USA (Camp et al., 1977).

P. markhami Sandberg, 1996: Athelginae, unidentified; Turks and Caicos Islands (Markham, 1978).

P. monoporus Morgan, 1987: *Bopyrissa* (?) sp., Pseudioninae; Irian Jaya, Indonesia (Haig and Ball, 1988). *Parapagurion calcincola* Shiino, 1933, Pseudioninae; Phuket, Thailand (Markham, 1985b). *Parathelges whiteleggei* Nierstrasz and Brender à Brandis, 1931, Athelginae; Irian Jaya, Indonesia (Haig and Ball, 1988).

P. oculatus (Fabricius, 1775): *Asymmetrione foresti* (Bourdon, 1968), Pseudioninae; Western Mediterranean (Bourdon, 1968).

P. oxyophthalmus Holthuis, 1959: *Parathelges piriformis* Markham, 1972, Athelginae; Caribbean coast, Colombia (Markham, 1978).

P. perspicax (Nobili, 1906): *Allathelges pakistanensis* Kazmi and Markham, 1999, Athelginae; Karachi, Pakistan (Kazmi and Markham, 1999).

P. robustus Forest and de Saint Laurent, 1967: *Pseudione biacuta* Bourdon, 1979, Pseudioninae; Uruguay (Bourdon, 1979).

P. subpilosus Henderson, 1888: *Pseudostegias otagoensis* Page, 1985, Athelginae; Otago, New Zealand (Page, 1985).

P. tortugae Schmitt, 1933: *Asymmetrione desultor* Markham, 1975 (?), Pseudioninae; Abrolhos Bank, Brazil (Bourdon, 1979). *Parapagurion imbricata* Markham, 1978, Pseudioninae; Cuba (Markham, 1978).

Strigopagurus boreonotus Forest, 1995: *Pseudostegias setoensis* Shiino, 1933, Athelginae; Chesterfield Islands (Markham, 1994).

Lithodidae

Dermaturus mandtii Brandt, 1850: *Pseudione giardi* Calman, 1898, Pseudioninae; Alaska (Markham, 1975). Unidentified branchial parasite, Pseudioninae?; Hokkaido, Japan (Minemizu, 2000).

Hapalogaster dentata (De Haan, 1844): *Pseudostegias hapalogasteri* Shiino, 1950, Athelginae; Mie, Japan (Shiino, 1950).

Lithodes murrayi Henderson, 1888: Unidentified, Pseudioninae?; Crozet Islands (Vinuesa, 1989).

L. santolla (Molina, 1872): unidentified, Pseudioninae?; Beagle Channel, Argentina (Vinuesa, 1989).

Neolithodes diomediae (Benedict, 1894): *Pseudione tuberculata* Richardson, 1904, Pseudioninae; Pampas, Argentina (Richardson, 1904); South Georgia (Vinuesa, 1989).

Paralomis granulosa (Jacquinot, 1847): *Pseudione tuberculata* Richardson, 1904, Pseudioninae; Beagle Channel, Argentina (Roccatagliata and Lovrich, 1999).

Paguridae

Anapagurus breviaculeatus Fenizia, 1937: *Athelges tenuicaudis* Sars, 1898, Athelginae; Mediterranean coast, Spain (García-Gómez, 1994).

A. chiroacanthus (Lilljeborg, 1856): *Pseudione hyndmanni* (Bate and Westwood, 1868), Pseudioninae; Denmark; English Channel (Bourdon, 1968). *Athelges tenuicaudis* Sars, 1898, Athelginae; Scandinavia; British Isles; France (Sars, 1898).

A. hyndmanni (Bell, 1846): *Athelges tenuicaudis* Sars, 1898, Athelginae; Atlantic coast, France (Bourdon, 1964).

A. japonicus Ortmann, 1892: unidentified branchial, Pseudioninae?; Sagami Bay, Japan (Miyake, 1978).

A. laevis (Bell, 1845): *Pseudione hyndmanni* (Bate and Westwood, 1868), Pseudioninae; English Channel; Spain (Bourdon, 1968). *Athelges paguri* (Rathke, 1843), Athelginae. Britain (Naylor, 1963).

Aniculus aniculus (Herbst, 1791): *Parathelges aniculi* (Whitelegge, 1897), Athelginae; Funafuti Atoll (Whitelegge, 1897).

Catapagurodes fragilis (Melin, 1939): unidentified abdominal, Athelginae?; Sagami Bay, Japan (Miyake, 1978).

Iridopagurus caribbensis (A. Milne Edwards, 1893): *Stegophryxus hyptius* Thompson, 1902, Athelginae; Western Florida, USA (García-Gómez, 1983).

I. iris (A. Milne Edwards, 1880): *Pseudionella* sp., Pseudioninae; Venezuela (Markham, 1978).

I. margaritensis García-Gómez, 1983: *Parathelges occidentalis* Markham, 1972, Athelginae; Venezuela (Markham, 1972). *Stegophryxus hyptius* Thompson, 1902, Athelginae; Curaçao (García-Gómez, 1983).

I. occidentalis (Faxon, 1893): unidentified; Cocos Island, Costa Rica (García-Gómez, 1983).

Iridopagurus sp.: *Asymmetrione desultor* Markham, 1975, Pseudioninae; Belize (Markham, 1988).

Lophopagurus (Lophopagurus) lacertosus (Henderson, 1888): unidentified branchial, Pseudioninae?; New Zealand (Forest et al., 2000). Unidentified abdominal, Athelginae?; New Zealand (Forest et al., 2000).

L. (L.) lacertosus (Henderson, 1888)?: *Pseudione hyndmanni* (Bate and Westwood, 1868), Pseudioninae; New Zealand (Page, 1985). *Athelges lacertosi* Pike, 1961, Athelginae; New Zealand (Page, 1985).

L. (L.) thompsoni (Filhol, 1885)?: *Athelges lacertosi* Pike, 1961, Athelginae; New Zealand (Pike, 1961).

L. (Australeremus) cooki (Filhol, 1883): *Athelges lacertosi* Pike, 1961, Athelginae; New Zealand (Page, 1985).

L. (A.) triserratus (Ortmann, 1892): *Pseudione intermedia* Nierstrasz and Brender à Brandis, 1932, Pseudioninae; Sagami and Misaki, Japan (McLaughlin and Gunn, 1992).

Manucomplanus unguatus (Studer, 1863): *Parathelges occidentalis* Markham, 1972, Athelginae; North Carolina, USA (Markham, 1972).

Pagurus aleuticus (Benedict, 1892): *Pseudione giardi* Calman, 1898, Pseudioninae; Alaska and Washington, USA (Markham, 1975).

P. annulipes (Stimpson, 1860): *Pseudionella markhami* (Adkison and Heard, 1978), Pseudioninae; North Carolina and

Georgia, USA (Adkison and Heard, 1978). *Stegophryxus hyptius* Thompson, 1902, Athelginae; North Carolina, USA; Gulf of Mexico (Markham, 1974).

P. arenisaxatilis Harvey and McLaughlin, 1991: *Stegophryxus* sp., Athelginae; Gulf of California, Mexico; Pacific coast, Costa Rica (Harvey and McLaughlin, 1991).

P. armatus (Dana, 1851): *Pseudione giardi* Calman, 1898, Pseudioninae; Washington, USA (Nyblade, 1974).

P. beringanus (Benedict, 1892): *Pseudione giardi* Calman, 1898, Pseudioninae; Washington, USA (Markham, 1975). *Athelges paguri* (Rathke, 1843), Athelginae; Norway to Belgium; Britain (Sars, 1898; Pérez, 1934).

P. brevidactylus (Stimpson, 1859): *Asymmetrione desultor* Markham, 1975, Pseudioninae; Caribbean coast, Colombia (Markham, 1988). *Pseudionella markhami* (Adkison and Heard, 1978), Pseudioninae; Caribbean coast, Colombia (Markham, 1988). *Parathelges foliatus* Markham, 1972, Athelginae; Barbados; Curaçao (Markham, 1978). *Parathelges piriformis* Markham, 1972, Athelginae; Bermuda (Markham, 1978). *Stegophryxus hyptius* Thompson, 1902, Athelginae; Florida, USA (Markham, 1978).

P. capillatus (Benedict, 1892): *Pseudione giardi* Calman, 1898, Pseudioninae; Washington, USA (Nyblade, 1974).

P. criniticornis (Dana, 1852): *Pseudionella deflexa* Bourdon, 1979, Pseudioninae; Southern Brazil (Bourdon, 1979).

P. cuanensis (Bell, 1845): *Athelges bilobus* Sars, 1898, Athelginae; Denmark; English Channel (Bourdon, 1967). *Athelges cladophorus* Gerstaecker, 1862, Athelginae; British Isles (Bonnier, 1900). *Athelges paguri* (Rathke, 1843), Athelginae; France (Hesse, 1876).

P. dubius (Ortmann, 1892): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Korea (Kim and Kwon, 1988). *Parathelges enoshimensis* Shiino, 1950, Athelginae; Korea (Kim and Kwon, 1988).

P. hirsutiusculus Dana, 1851: *Pseudione giardi* Calman, 1898, Pseudioninae; Alaska and Washington, USA (Markham, 1975).

P. japonicus (Stimpson, 1859): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Seto, Japan (Shiino, 1958).

P. kulkani Sankoli, 1962: *Parathelges neotenuicaudis* (Shyamasundari et al., 1993), Athelginae; Eastern India (Shyamasundari et al., 1993); Karachi, Pakistan (Markham and Kazmi, 1998).

P. lanuginosus De Haan, 1849 (s. l.): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Tokyo Bay, Japan (Shiino, 1958).

P. longicarpus Say, 1817: *Asymmetrione desultor* Markham, 1975, Pseudioninae; North Carolina, USA (Markham, 1975). *Stegophryxus hyptius* Thompson, 1902, Athelginae; Massachusetts to Georgia, USA (Markham, 1974).

P. macLaughlinae García-Gómez, 1982: *Stegophryxus hyptius* Thompson, 1902, Athelginae; Florida, USA (Markham, 1988).

P. maculosus Komai and Imafuku, 1996: *Athelges takanoshimensis* Ishii, 1914, Athelginae; Honshu, Japan (Nagasawa et al., 1996).

P. megalops (Stimpson, 1858); unidentified; Sagami Bay, Japan (Miyake, 1978).

P. middendorffi Brandt, 1851: *Pseudione hyndmanni* (Bate and Westwood, 1868)?, Pseudioninae; Hokkaido, Japan (Shiino, 1958). *Athelges takanoshimensis* Ishii, 1914, Athelginae; Eastern Russia; Japan; Korea (Kim and Kwon, 1988).

P. ochotensis Brandt, 1851: *Pseudione giardi* Calman, 1898, Pseudioninae; Alaska, USA (Markham, 1975).

P. pectinatus (Stimpson, 1858): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Japan; Korea (Kim and Kwon, 1988).

P. prideauxii Leach, 1815: *Pseudione hyndmanni* (Bate and Westwood, 1868)?, Pseudioninae; Scotland (Henderson, 1886). *Athelges prideauxii* Giard and Bonnier, 1890, Athelginae; Scotland; France; Italy (Pike, 1953). *Athelges* sp., Athelginae; Norway (Samuelson, 1970).

P. provenzano Forest and de Saint Laurent, 1967: *Asymmetrione desultor* Markham, 1975, Pseudioninae; Antigua; Bonaire; Curaçao (Markham, 1978). *Parathelges piriformis* Markham, 1972, Athelginae; Bahamas (Markham, 1978). *Stegophryxus hyptius* Thompson, 1902, Athelginae; Curaçao (Markham, 1978).

P. pubescens (Krøyer, 1838): *Pseudione hyndmanni* (Bate and Westwood, 1868), Pseudioninae; Norway; Iceland; Faeroe Islands; Britain (Bourdon, 1968).

P. stimpsoni (A. Milne Edwards and Bouvier, 1893): *Asymmetrione desultor* Markham, 1975, Pseudioninae; Florida, USA (Markham, 1975). *Pseudionella markhami* (Adkison and Heard, 1978), Pseudioninae; Caribbean coast, Colombia (Markham, 1988). *Stegophryxus hyptius* Thompson, 1902, Athelginae; Florida, USA (Markham, 1974).

P. brachiomastus (Thallwitz, 1892): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Korea (Kim and Kwon, 1988).

P. venturensis Coffin, 1957: *Pseudione* sp., Pseudioninae; California, USA (Miller, 1975).

P. vetaultae Harvey and McLaughlin, 1991: *Stegophryxus* sp., Athelginae; Pacific coast, Costa Rica (Harvey and McLaughlin, 1991).

Pagurus sp.: *Pseudione intermedia* Nierstrasz and Brender à Brandis, 1932, Pseudioninae; Misaki, Japan (Shiino, 1972).

Pagurus sp.: *Pseudionella attenuata* Shiino, 1949, Pseudioninae; Seto, Japan (Shiino, 1949).

Pagurus sp.: *Anathelges resupinatus* (Müller, 1871), Athelginae; Florianópolis, Brazil (Müller, 1871).

Pagurus sp.: *Parathelges enoshimensis* Shiino, 1950, Athelginae; Enoshima, Japan (Shiino, 1950).

Pagurus sp.: *Stegophryxus thompsoni* Nierstrasz and Brender à Brandis, 1931, Athelginae; Valparaíso, Chile (Nierstrasz and Brender à Brandis, 1931).

Pagurus sp.: *Parathelges whiteleggei* Nierstrasz and Brender à Brandis, 1931, Athelginae; Java Sea (Nierstrasz and Brender à Brandis, 1931).

Parapagurodes constans (Stimpson, 1858): *Athelges takanoshimensis* Ishii, 1914, Athelginae; Tokyo Bay, Japan (Shiino, 1958).

P. laurentae McLaughlin and Haig, 1973: *Stegophryxus hyphalus* Markham, 1974, Athelginae; California, USA; Baja California, Mexico (Markham, 1974).

P. makarovi McLaughlin and Haig, 1973: *Stegophryxus hyphalus* Markham, 1974, Athelginae; California, USA; Baja California, Mexico (Markham, 1974).

Propagurus haigae (McLaughlin, 1997): Unidentified branchial, Pseudioninae?; New Caledonia (McLaughlin and de Saint Laurent, 1998).

Pylopagurus unguatus (Studer, 1883): *Parathelges occidentalis* Markham, 1972, Athelginae; North Carolina, USA (Markham, 1972).

Tomopagurus cokeri (Hay, 1917): Athelginae, unidentified; Quintana Roo, Mexico (Markham, 1978).

Pagurid, unidentified: *Anathelges mossambica* Barnard, 1956, Athelginae; Mozambique (Barnard, 1956).

Pagurid, unidentified: *Stegophryxus minutus* Markham, 1992, Athelginae; Hong Kong (Markham, 1992).

Family Parapaguridae

Oncopagurus bicristatus (A. Milne Edwards, 1880): *Pleurocyptella paguri* Bourdon, 1979?, Pseudioninae; Azores (Bourdon, 1981).

O. monstrosus (Alcock, 1905): *Bopyrophryxus branchi abdominalis* Codreanu, 1965, Bopyrophryxinae; Kei Islands, Indonesia (Codreanu, 1965).

Parapagurus pilosimanus Smith, 1879: *Pleurocyptella paguri* Bourdon, 1979, Pseudioninae; Azores (Bourdon, 1979).

Parapagurus sp.: *Parapagurion imbricata* Markham, 1978, Pseudioninae; Caribbean coast, Colombia (Markham, 1978).

Pylochelidae

No records known.

Discussion

It is difficult to infer many generalisations about the occurrence of the parasites considered, because they do not fit into discernible patterns. Of the species of the Pseudioninae known to infest paguroids, most belong to genera not known from hosts outside of that superfamily. The exceptions are the nine species of *Pseudione*, among whose other species (totalling more than 50) are parasites of many other anomurans, numerous thalassinideans and some deep-water carideans; and *Pleurocyptella paguri* Bourdon, known from one or two species of *Parapagurus*, whose congeneric species are all parasites of galatheids. Despite their markedly different appearance from other paguroids, the lithodids bear parasites closely related to those of hosts in other paguroid families; all of their branchial parasites are assignable to *Pseudione* (*P. giardi* Calman being reported as a parasite of both a lithodid and several species of hermit crabs); and the single lithodid-infesting abdominal bopyrid, *Pseudostegias hapalogasteri* Shiino, is in a genus whose other species infest hermit crabs. Most genera of parasites containing more than single species infest both diogenids and pagurids, but all seven species of the pseudionine genus *Bopyrissa* infest only diogenids, while all four species of the athelgine genus *Stegophryxus* infest only pagurids. The most widespread species is *Pseudione hyndmanni* (Bate and Westwood), reported from six host species of pagurids in

western Europe (Bourdon, 1968), another in New Zealand (Page, 1985), and possibly one in Japan (Shiino, 1958). It seems to be an analogue of the closely similar *Pseudione giardi* Calman, which infests five species of *Pagurus* and the lithodid *Dermaturus mandtii* in northwestern North America (Markham, 1975; Nyblade, 1974). Among abdominal parasites, *Athelges* spp. infest many different pagurids in Europe (Sars, 1898; Bourdon, 1967), while *A. takanoishimensis* Ishii infests ten species of pagurids in the western Pacific (Kim and Kwon, 1988; Nagasawa et al., 1996; Shiino, 1958).

Acknowledgments

I am deeply indebted to Patsy McLaughlin for patiently and thoroughly reading the list of paguroid names, remedying my errors and omissions and providing the currently accepted names of the species. Rafael Lemaître and Christopher Boyko furnished elusive nomenclatorial information, while Rafael Lemaître and Chris Tudge provided necessary editorial assistance. Anonymous reviewers made valuable suggestions for the improvement of the manuscript.

References

- Adkison, D.L., and Heard, R.W. 1978. Description of a new genus and species of Pseudioninae (Isopoda: Bopyridae) parasite of the hermit crab *Pagurus annulipes* (Stimpson) from North Carolina. *Proceedings of the Biological Society of Washington* 91: 408–417.
- Altès, J. 1962. Sur quelques parasites et hyperparasites de *Clibanarius erythropus* (Latreille) en Corse. *Bulletin de la Société de Zoologie de France* 87: 88–97.
- Babić, K. 1912. Über einen Athelges von Pelagosa. *Zoologischer Anzeiger, Leipzig* 40: 176–178.
- Barnard, K.H. 1950. Descriptive catalogue of South African decapod Crustacea (crabs and shrimps). *Annals of the South African Museum* 38:1–837.
- Barnard, K.H. 1955. Additions to the fauna-list of South African Crustacea and Pycnogonida. *Annals of the South African Museum* 43: 1–107.
- Barnard, K.H. 1956. Further additions to the crustacean fauna-list of Portuguese East Africa. *Memórias do Museu Dr. Alvaro de Castro* 4: 3–23.
- Bonnier, J. 1900. Contribution à l'étude des Épicarides. Les Bopyridae. *Travaux de l'Institut Zoologique de Lille et du Laboratoire de Zoologie Maritime de Wimereux* 8:1–478.
- Bourdon, R. 1964. Épicarides et rhizocéphales du Bassin d'Arcachon. *Procès Verbaux de la Société Linnéenne Bordeaux* 101: 1–7.
- Bourdon, R. 1967. Données complémentaires sur les épicarides et les rhizocéphales de Roscoff. *Bulletin de l'Académie de la Société de Sciences Lorraines* 6: 281–286.
- Bourdon, R. 1968. Les Bopyridae des mers Européennes. *Mémoires du Muséum National d'Histoire Naturelle de Paris, Nouvel Série* (A) 50 (2): 77–424.
- Bourdon, R. 1979. Campagne de la Calypso au large des côtes Atlantiques de l'Amérique du Sud (1961–1962) I. 32. Crustacés Isopodes: Bopyridae parasites de Pagures. *Résultats scientifiques des Campagnes de la Calypso* 9: 139–144.
- Bourdon, R. 1981. Bopyriens nouveaux pour la faune européenne de l'Atlantique (Isopoda Epicaridea). *Bulletin du Muséum National d'Histoire Naturelle de Paris* (4) 3 (Section A, 2): 615–634.

- Brian, A., and Dartevelle, E. 1941. Sur un épicaride nouveau du Congo: *Pseudione Brandaoui* nov. sp. *Revue de Zoologie et Botanique d'Afrique (Tervuren)* 34: 348–352.
- Brusca, R. C. 1980. *Common intertidal invertebrates of the Gulf of California. Second Edition.* University of Arizona: Tucson. 513 pp.
- Camp, D.K., Whiting, N.H., and Martin, R.E. 1977. Nearshore marine ecology at Hutchinson Island, Florida: 1971–1974. V. Arthropoda. *Florida Marine Research Publications* 25: 1–63.
- Codreanu, R. 1940. Sur un épicaride nouveau, *Parathelges racovitza* n. sp., ectoparasite de la Mer Noire. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences de Paris* 210: 679–681.
- Codreanu, R. 1961. Crustacei paraziți cu afinități indo-pacifice în Marea Neagră. *Hidrobiologia* 3: 133–146.
- Codreanu, R. 1965. Sur un bopyride nouveau, *Bopyrophryxus branchi-abdominalis* nov. gen. nov. sp., parasite de *Parapagurus monstrosus* des îles Kei et type de la sous-famille nouvelle des Bopyrophryxinae nov. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences de Paris* 261 (Groupe 12): 1895–1897.
- Codreanu, R. 1968. Y a-t-il des especes biologiques (jumelles) chez les épicarides et les rhizocéphales? *Travaux Muzeul national Istorie Naturala "Grigore Antipa," Bucuresti* 8: 601–614.
- Codreanu, R., and Codreanu, M. 1963. Sur plusieurs bopyriens parasites branchiaux des anomoures de la Mer Noire, de la Méditerranée et du Viet-Nam. *Rapports et Procès verbaux de réunions de la Commission internationale pour l'Exploration scientifique de la mer Méditerranée* 17: 283–285.
- Codreanu, R., Codreanu, M. and Pike, R.B. 1965. Sur deux bopyriens parasites de pagures recueillis par M. A. Horridge dans la mer Rouge et sur leur asymétrie. *Crustaceana* 9 (3): 225–244.
- Danforth, C.G. 1971. Two bopyrids (Isopoda) from New Guinea. *Bulletin of the Southern California Academy of Sciences* 70: 99–102.
- Dunbar, S.G. and Coates, M. 2000. Range extension and new host records of the ectoparasite *Pseudostegias setoensis* Shiino, 1933 (Crustacea: Isopoda: Bopyridae). *Transactions of the Royal Society of South Australia* 124: 49.
- Forest, J., de Saint Laurent, M., McLaughlin, P.A., and Lemaitre, R. 2000. The marine fauna of New Zealand: Paguridea (Decapoda: Anomura) exclusive of the Lithodidae. *NIWA Biodiversity Memoir* 114: 1–250.
- García-Gómez, J. 1983. Revision of *Iridopagurus* (Crustacea: Decapoda: Paguridae) with the descriptions of new species from American waters. *Bulletin of Marine Science* 33: 10–54.
- García-Gómez, J. 1994. The systematics of the genus *Anapagurus* Henderson, 1886, and a new genus for *Anapagurus drachi* Forest, 1966 (Crustacea: Decapoda: Paguridae). *Zoologische Verhandlungen* 295: 1–13.
- Haig, J., and Ball, E.E. 1988. Hermit crabs from north Australian and eastern Indonesian waters (Crustacea: Decapoda: Anomura: Paguroidea) collected during the 1975 *Alpha Helix* Expedition. *Records of the Australian Museum* 40: 11–196.
- Harvey, A.W., and McLaughlin, P.A. 1991. Two new hermit crabs of the genus *Pagurus* (provenzano group) (Crustacea, Anomura, Paguridae) from the eastern Pacific, with notes on their ecology. *Contributions in Science* 425: 13–21, figs 1–3.
- Henderson, J.R. 1886. The decapod and schizopod Crustacea of the Firth of Clyde. *Proceedings and Transactions of the Natural History Society of Glasgow* 3: 315–353.
- Hesse, M. 1876. Description des Crustacés rares ou nouveaux des côtes de France. Nouvelles observations sur les isopodes sédentaires: Athelgue et Pleurocrypte. *Annales des Sciences Naturelles, Zoologie et Paléontologie* (6) 4 (Article 2): 1–48.
- Jones, D.S. and Morgan, G.J. 1994. *A field guide to crustaceans of Australian waters.* Reed: Chatswood. 216 pp.
- Kazmi, Q., and Markham, J.C. 1999. *Allathelges pakistanensis*, new genus, new species, a bopyrid isopod from Karachi, Pakistan, with a review of the Athelginae recorded from the Indian Ocean. *Journal of Crustacean Biology* 19: 879–885.
- Kim, H.S., and Kwon, D.H. 1988. Bopyrid isopods parasitic on decapod crustaceans in Korea. *The Korean Journal of Systematic Zoology. Special Issue* 2: 199–221.
- Lemos de Castro, A. 1965. Crustáceos isópodos epicarídeos do Brasil. I: Descrição de uma espécie do gênero "*Pseudostegias*" Shiino (Isopoda, Bopyridae). *Revista Brasileira de Biologia* 25: 105–108.
- Markham, J.C. 1972. Four new species of *Parathelges* Bonnier, 1900 (Isopoda, Bopyridae), the first record of the genus from the western Atlantic. *Crustaceana Supplement* 3: 57–78.
- Markham, J.C. 1974. Parasitic bopyrid isopods of the amphi-American genus *Stegophryxus* Thompson with the description of a new species from California. *Bulletin of the Southern California Academy of Sciences* 73: 33–41.
- Markham, J.C. 1975. Two new species of *Asymmetrione* (Isopoda, Bopyridae) from the Western Atlantic. *Crustaceana* 29 (3): 255–265.
- Markham, J. C. 1978. Bopyrid isopods parasitizing hermit crabs in the northwestern Atlantic Ocean. *Bulletin of Marine Science* 28: 102–117.
- Markham, J.C. 1979. Epicaridean isopods of Bermuda. *Bulletin of Marine Science* 29: 522–529.
- Markham, J.C. 1982. Bopyrid isopods parasitic on decapod crustaceans in Hong Kong and southern China. Pp. 325–391 in: Morton, B. S., and Tseng, C. K. (eds), *Proceedings of the First International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China*, 1. Hong Kong University Press: Hong Kong.
- Markham, J.C. 1985a. A new species of *Asymmetrione* (Isopoda: Bopyridae) infesting the hermit crab *Isocheles pilosus* (Holmes) in southern California. *Bulletin of the Southern California Academy of Sciences* 84: 104–108.
- Markham, J.C. 1985b. Additions to the bopyrid fauna of Thailand. *Zoologische Verhandlungen* 224: 1–63.
- Markham, J.C. 1988. Descriptions and revisions of some species of Isopoda Bopyridae of the north western Atlantic Ocean. *Zoologische Verhandlungen* 246: 1–63.
- Markham, J.C. 1992. Second list of additions to the Isopoda Bopyridae of Hong Kong. Pp. 277–302 in: Morton, B. (ed.), *The marine flora and fauna of Hong Kong and southern China* 3. Volume 1. Hong Kong University Press: Hong Kong.
- Markham, J.C. 1994. Crustacea Isopoda: Bopyridae in the MUSORSTOM collections from the tropical Indo-Pacific I. Subfamilies Pseudioninae (in part), Argeiinae, Orbioninae, Athelginae and Entophilinae. Pp. 225–253. in: Crosnier, A. (ed.), *Résultats des Campagnes MUSORSTOM, volume 10. Mémoires du Muséum national d'Histoire Naturelle, Paris* 161.
- Markham, J.C., Donath-Hernandos, F.E., Villalobos-Hiriart, J.L., and Diaz-Barriga, A.C. 1990. Notes on the shallow-water marine Crustacea of the Caribbean coast of Quintana Roo, Mexico. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México, Zoología* 61: 405–446.
- Markham, J.C., and Kazmi, Q.B. 1998. Extension of range and description of male of the bopyrid isopod *Parathelges neotenuicaudalis* (Shyamasundari et al., 1993) from Karachi, Pakistan. *Pakistan Journal of Marine Sciences* 7: 147–152.
- Martin, J.W., and Davis, G.E. 2001. An updated classification of the Recent Crustacea. *Natural History Museum of Los Angeles County, Science Series* 39: 1–124.

- McLaughlin, P.A., and de Saint Laurent, M. 1998. A new genus for four species of hermit crabs formerly assigned to the genus *Pagurus* Fabricius (Decapoda: Anomura: Paguridae). *Proceedings of the Biological Society of Washington* 111: 158–187.
- McLaughlin, P.A., and Gunn, S.W. 1992. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species. Part IV. *Lophopagurus* McLaughlin and *Australeremus* McLaughlin. *Memoirs of the Museum of Victoria* 53: 43–99.
- Miller, M.A. 1975. Phylum Arthropoda: Crustacea, Tanaidacea and Isopoda. Pp. 277–312 in: Smith, R. I. and Carlton, J. T. (eds), *Light's manual: Intertidal invertebrates of the central California coast*. University of California Press: Berkeley.
- Minemizu, R. 2000. [Marine decapod and stomatopod crustaceans mainly from Japan]. Bunichi Sogo Shuppan: Tokyo. 344 pp. [In Japanese]
- Miyake, S. 1978. *The crustacean Anomura of Sagami Bay collected by His Majesty the Emperor of Japan*. Biological Laboratory Imperial Household: Tokyo. 200 pp.
- Müller, F. 1871. Bruchstücke zur Naturgeschichte der Bopyriden. *Jenaische Zeitschrift für Medizin und Naturwissenschaft* 6: 53–73.
- Nagasawa, K., Lützen, J., and Kado, R. 1996. Parasitic Cirripedia (Rhizocephala) and Isopoda from brachyuran and anomuran crabs of the Pacific coast of northern Honshu, Japan. *Bulletin of the Biogeographical Society of Japan* 51: 1–6.
- Naylor, E. 1963. Epicaridea. Pp. 148–149 in: Bruce, J. R., Colman, J. S. and Jones, N. S. (eds), *Marine fauna of the Isle of Man*. Liverpool University Press: Liverpool.
- Nierstrasz, H.F., and Brender à Brandis, G.A. 1931. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. 57. Epicaridea 2. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i København* 91: 147–225.
- Nyblade, C.F. 1974. *Coexistence in sympatric hermit crabs*. Ph. D. dissertation. University of Washington: Seattle. 241 pp.
- Page, R.D.M. 1985. Review of the New Zealand Bopyridae (Crustacea: Isopoda: Epicaridea). *New Zealand Journal of Zoology* 12: 185–212.
- Pérez, C. 1934. Notes sur les Épicarides et les Rhizocéphales des côtes de France. VIII. Infection simultanée des pagures par un *Athelges* et un Rhizocéphale. *Archives de Zoologie expérimentale générale* 75: 541–565.
- Pike, R.B. 1953. The bopyrid parasites of the Anomura from British and Irish waters. *Journal of the Linnean Society of London (Zoology)* 42: 219–237.
- Pike, R.B. 1961. A new bopyrid parasite collected by the Chatham Islands 1954 Expedition. *New Zealand Department of Scientific Industries Research Bulletin* 139, *Biological Results of the Chatham Islands 1954 Expedition*. Part 5: 221–223.
- Richardson, H. 1904. Contributions to the natural history of the Isopoda. *Proceedings of the United States National Museum* 27: 1–89.
- Roccatagliata, D., and Lovrich, G.A. 1999. Infestation of the false king crab *Paralomis granulosa* (Decapoda: Lithodidae) by *Pseudione tuberculata* (Isopoda: Bopyridae) in the Beagle Channel, Argentina. *Journal of Crustacean Biology* 19: 720–729.
- Samuelson, T.J. 1970. The biology of six species of Anomura (Crustacea, Decapoda) from Raunefjorden, western Norway. *Sarsia* 45: 25–52.
- Sars, G.O. 1898. An account of the Crustacea of Norway with short descriptions and figures of all the species. Volume II. Isopoda. Part XI, XII. Oniscidae (concluded), Bopyridae, Dajidae. Pp. 185–232. Bergen Museum: Bergen.
- Shiino, S.M. 1933. Bopyrids from Tanabe Bay. *Memoirs of the College of Science, Kyoto Imperial University (B)* 8 (3, Article 8): 249–300.
- Shiino, S.M. 1949. On two genera of Bopyridae found in Japan. *Bulletin of the Biogeographical Society of Japan* 14 (11): 57–63.
- Shiino, S.M. 1950. Notes on some new bopyrids from Japan. *Mie Medical Journal* 1 (2): 151–167.
- Shiino, S.M. 1958. Note on the bopyrid fauna of Japan. *Report of the Faculty of Fisheries, Prefectural University of Mie* 3: 29–73.
- Shiino, S.M. 1972. [The Epicaridea (list of species) from Japan]. *Kansai Shizenkagaku* 24: 7–10. [In Japanese]
- Shyamasundari, K., Hanamantha-Rao, K., Jalajakumari, C., and Mary, A. 1993. A new bopyrid isopod *Athelges neotenuicaudis* (Crustacea: Isopoda: Epicaridea) parasitic on *Pagurus kulkarnii* from Visakhapatnam Coast, India. *Boletín Chileno de Parasitología* 48 (3–4): 60–63.
- Vinuesa, J.H. 1989. Efectos e incidencia del parasitismo en la centolla (*Lithodes santolla*) y centellón (*Paralomis granulosa*) del Canal Beagle. *Physis (Buenos Aires)* 47:45–51
- Whitelegge, T. 1897. The atoll of Funafuti, Ellice Group: its zoology, botany, ethnology and general structure. VI. The Crustacea. *Australian Museum, Sydney, Memoir* 3: 127–151
- Williams, J.D. and Boyko, C.B. 1999. A new species of *Pseudostegias* Shiino, 1933 (Crustacea: Isopoda: Bopyridae: Athelginae) parasitic on hermit crabs from Bali. *Proceedings of the Biological Society of Washington* 112: 714–721.